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Effects of nitrogen content on growth and hydraulic characteristics of peach (*Prunus persica* L.) seedlings under different soil moisture conditions

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Abstract: A pot experiment was conducted to investigate the effects of nitrogen content [N_1 (no fertilizer), N_2 (0.15 g·kg^{-1}), and N_3 (0.3 g·kg^{-1})] on the growth and the hydraulic characteristics of peach seedlings under different soil moisture conditions (W_1, W_2 and W_3, in which the soil water content was 45% to 55%, 60% to 70%, and 75% to 80% of the field water capacity, respectively) by using a specialized high pressure flow meter with a root chamber and a coupling, which was connected to plant organs. Leaf area and leaf hydraulic conductivity (K_L) increased significantly in the seedlings because of increased soil moisture and N

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content. K_L increased with leaf area. A linear correlation was documented between K_L and leaf area. K_L was higher in the morning and began to decline sharply after 16:00, at which K_L declined after an initial increase. Soil moisture and N content enhanced shoot (K_s) and root (K_r) hydraulic conductivities, thereby improving the low soil moisture condition to a large extent. K_s and K_r of the seedlings were reduced by 32% and 27% respectively in N_1, and by 14.7% and 9.4%, respectively in N_2, and both in W_1, compared with the control treatment. N_3 had no significant effect on K_s and K_r under similar conditions. Linear negative correlations were observed between K_r and the excised root diameter as well as between K_s and the shoot stem diameter. The shoot-to-root ratio increased with increase in N content. The shoot-to-root ratio in N_3 was increased by 14.37%, compared with N_1 in W_1 as well as by 12% and 4.39% in W_2 and W_3, respectively. Knowledge of the effects of soil moisture and N fertilizer on hydraulic characteristics and growth is important. Our results provide basic guidelines for the implementation of water-saving irrigation and fertilization management of nursery stock.

Keywords: nitrogen, Hydraulic conductivity, growth, WUE, *Prunus persica* L.

Introduction

In arid and semi-arid regions, plants are often confronted with various extremely challenging environmental conditions such as drought or nutrient deficiency during their lifespan. Transport of water and nutrients by plants is an important function for plant growth, which is affected by the hydraulic characteristics of plant organs and the absorption functions of roots (Taiz and Zeiger 2002; Yasutake et al. 2011). Seedlings grown with large inputs of fertilizer have shown high survival and growth under field conditions (Villar-Salvador et al. 2004; Oliet et al. 2009), but outcomes have been different in environments with severe water limitations (Trubat et al. 2008). Drought stress limits or reduces seedling growth and affects xylem hydraulic conductivity

(Brodribb and Hill 1999; Triboulot et al. 2002; Ladjal et al. 2005). Excessive fertilization may influence seedling physiology in ways that exacerbate drought-related injury (Kleczewski et al. 2010). Soil nutrient availability influences patterns of carbon allocation (Hikosaka et al. 2005; Müller et al. 2010) and might also affect the hydraulic functions, and consequently the water relations of plants (Bucci et al. 2006).

The capacity to transport water throughout a tree can be determined by measuring hydraulic conductivity. Of the variety of environmental factors which affect plant hydraulic conductivity, drought stress and nutrient deficiency attract most attention. Generally, water deficiency causes reductions in stomatal and root hydraulic conductivity, compromising the water status of the plant (Siemens et al. 2004). The shoot hydraulic conductivity (Ks) can be influenced chiefly by the surrounding nutrient conditions under given evapotranspiration demands, soil water potentials, and soil temperatures (Clarkson et al. 2000; Steudle 2000a, 2000b; Zhao et al. 2004). Root hydraulic conductivity (Kr) declines with reduced soil water content when plants suffer water stress in soil (Kang and Zhang 1997). Plants influenced by soil drought stress can respond in a variety of ways. The most common response arises directly from the decline in xylem water potential, increase in tension, and resulting decline in xylem hydraulic conductivity (Lo Gullo et al. 1998; Zhang et al. 2003; Vandeleur et al. 2009), which eventually leads to xylem embolism due to moisture transport barriers. It has been proven that a deficiency of nitrogen (N) causes a reduction in the hydraulic conductivity of cells and single roots. Some studies have found that the addition of nutrient elements changed the xylem vessel diameter, thus affecting the conductivity of the vessel. N fertilization significantly alters several components of hydraulic architecture: specific conductivity of terminal stems increases with N additions (Bucci et al. 2006). Hydraulic conductivity of stems can be greatly affected by fertilization and stem hydraulic conductivity can increase 2.5-fold with N enrichment (Lovelock et al. 2004). Kr can be increased by applying N fertilizer (Lovelock et al. 2006).

Root growth potential and root hydraulic conductivity increase with N availability (Singh and Sale 2000; Trubat et al. 2006). As a result, the ability to capture soil water can be enhanced by fertilizing seedlings (Reinbott and Blevins 1999). Soil nutrient availability influences the morpho-functional and biomass allocation patterns of development in plants. Previous studies have reported changes in plant morphology and physiological traits as a consequence of different nutrient conditions (Villar-Salvador et al. 2004; Barigah et al. 2006; Trubat et al. 2006). This can be crucial in degraded areas with low soil fertility (Valdecantos et al. 2006), especially in arid and semi-arid areas, drought is often associated with low soil nutrient availability. Species tend to adapt to environmental conditions by different morphological and physiological adjustments (Wood 2005; Hernández et al. 2009). N fertilizer stress may cause change in growth, physiology and water use of plants (Radin and Matthews 1989; Passioura 2002; Lovelock et al. 2006; Cossania et al. 2012; Li et al. 2010). N deficient plants commonly change their biomass accumulation and allocation patterns (Poorter et al. 2000; Rubio et al.

2003), which may result in decreased demand for water and greater ability to endure drought. However, there are few studies on hydraulic conductivity characteristics of seedlings and its relationship with growth under different N concentrations and soil moisture conditions.

Water uptake by roots can be regulated by physical and physiological processes (Steudle 2000b, 2001) and hydraulic properties of roots vary with species and environmental conditions. The water uptake ability of plant roots and hydraulic characteristics, especially in seedling stage, has received much attention by plant physiologists because seedlings are too weak to survive in extreme suboptimal conditions. Therefore, great importance attaches to study of the theory and practice of the effects of N nutrition on plant hydraulic characteristics under conditions of soil drought. The objective of this study was to investigate growth characteristics of peach seedlings and the effect of N nutrition on leaf, root and shoot hydraulic characteristics under different soil moisture conditions. Understanding of the effect of interactions between N nutrition and soil drought on hydraulic characteristics is anticipated to provide useful information for breeding cultivars of crops with increased water use efficiency for cultivation in semi-arid regions.

Materials and methods

Experimental materials

The experiment was conducted from 1 March 2007 to 27 October 2007 under a rain shelter with natural light conditions at the Irrigation Experimental Station of Northwest A & F University, Yangling, Shaanxi, China (latitude 34°18′ N, longitude 108°24′ E, 521 m, a.s.l.). The site is semi-arid with average day and night temperatures of 29 and 20 ℃ and relative humidity of 30%–60%. The photon flux density ranged from 450 to 800 μmol·m^{-2}·s^{-1}.

Our experimental soil was topsoil (0-20 cm) of the cultivated horizon (heavy loam) that was naturally air-dried and passed through a 2 mm sieve. The following soil characteristics were measured: soil pH, 8.14, organic matter content, 10.92 g·kg^{-1}; total N, 0.89 g·kg^{-1}; total P, 0.72 g·kg^{-1}; total K, 13.8 g·kg^{-1}; available N content, 55.93 mg·kg^{-1}; available P, 28.18 mg·kg^{-1}; K, 102.30 mg·kg^{-1}; and soil water content at the field water capacity, 24% (on a mass basis). We placed the mixed cultivated soil (heavy loam: sand: vermiculite weight ratio = 8:1:1) in pots at bulk density of 1.3 g·cm^{-3} to prevent surface soil hardening from irrigation and improve soil permeability.

One-year-old peach seedlings (*Prunus persica* L.) were used as test materials. Homogeneous peach seedlings with normal growth were selected and soaked in rooting powder solution (IBA, Indole butyric acid, Zhengzhou Sun Rain Biological Products Co., Ltd., China) for 30 min to promote rapid growth and development of new roots. The seedlings were then transplanted into a pot (25 cm in inner diameter at the bottom, 30 cm in inner diameter at the top edge, and 30 cm in depth). Six uniform holes were drilled at the bottom of the pot and a thick layer of fine sand (1 kg) was paved to provide better aeration condi-

tions for the seedlings. During the pot experiment, all seedlings were initially watered until the field capacity was reached after they were transplanted.

Experimental design

We evaluated the effects of water and N treatments. Three water treatments were used: water-stressed (W_1), medium-watered (W_2), and well-watered (W_3) treatments, in which the soil water content was 45%–55%, 60%–70%, and 75%–80% of the field water capacity, respectively. Three N fertilizer treatments were evaluated: no fertilizer (N_1), medium amount of fertilizer (N_2, 0.15 g·kg^{-1} soil), and large amount of fertilizer (N_3, 0.3 g·kg^{-1} soil). According to the local crop irrigation regime, we selected the W_2N_2 treatment as the control (CK) treatment. N was supplied as urea, which was applied with analytical reagent. N fertilizer was applied according to the disposable method. N was applied to the pots in solution because this enabled even distribution of fertilizer to the soil by using a specific amount of water based on the field capacity. Each treatment was replicated thrice and 27 pots total were involved in this experiment.

Measurements

K measurements
Seedlings were brought into the laboratory for measurement. Hydraulic conductivity (K) was measured with a HPFM (Dynamax Inc., Houston, TX, USA) for the excised root system (K_r), shoot (K_s) and leaf (K_L). Shoots were cut at 40 mm above the soil surface. K was measured by transient pressurization of the HPFM from a supply of compressed N, which forced water from an enclosed tank into the severed sample (Tyree et al. 1998). The water pressure was increased from 0 to 500 kPa over 90s. The mass flow rate of water into the sample and applied pressure was measured by the HPFM every 5 s. Flow rate was plotted as a function of pressure and the hydraulic conductivity (K) of the sample was given by the slope of the linear portion of the graph as determined by linear regression (Smith and Roberts 2003). The K value per unit surface area of sample was then calculated. Measurement of leaf hydraulic conductivity (K_L) is illustrated in Fig. 1.

Fig. 1: Measurement of Leaf hydraulic conductivity (K_L)

Leaf transpiration rate and soil moisture content
Transpiration rate (T_r) was measured using a LI-6400 portable photosynthesis device (LI-6400, Li-Cor, Lincoln, Nebraska,

USA). Daily transpiration and evapotranspiration of the young peach trees were determined by the weighing method. Seedling pots were weighted daily at 7:00 pm. The soil water content of each pot was measured weekly from the beginning of March until the end of May by using a moisture meter type HH2, sensor Theta Probe type ML2x, (Delta-T Devices Ltd, UK). Seedling pots were marked to show three layers (top, middle, and bottom layers) and three holes were punched in the middle of each layer for determination of soil moisture content. The holes were sealed with tape immediately after each measurement to reduce water loss. The volumetric soil water content was calculated as the average of three measurements.

Diameter, root length and dry mass
Seedling root diameters and lengths were measured with a vernier calliper and a steel measuring tape. Seedlings were harvested at the end of the experiment for assessment of dry biomass accumulation. Roots and shoots were separately harvested. Plant material was initially dried at 105 °C for 30 min, and then dried at 65–75 °C to constant weight. WUE was defined as the amount of total biomass (shoot plus root dry mass) per unit of water used (Li et al. 2007).

Statistical analysis
The data were analyzed by analysis of variance (ANOVA) with SAS software (SAS, Version 8.1, SAS Institute Inc., USA). ANOVA considered water treatment and N level as the main effects and interaction. All the treatment means were compared for significant differences using Duncan's multiple range tests at the significant level of $P_{0.05}$ with the SAS for Windows software package.

Results

Leaf hydraulic conductivity

Effect of soil water content and N on leaf hydraulic conductivity (K_L), and correlation between K_L and leaf area
Soil water and N content significantly affected leaf hydraulic conductivity (K_L) and leaf area (Fig. 2). K_L of the peach seedlings increased with soil water content, but no significant relationship was observed between water content (W_1 and W_2) and K_L. At W_3, K_L increased by 28% over the value recorded at W_1. Leaf area also increased with increasing soil water content. Under different N treatments, K_L and leaf area increased with increasing N applications. A small increase was also noted in leaf area. K_L peaked at N_3, At N_2 and N_3 treatments, K_L increased by 10 and 20%, respectively. K_L increased with increasing leaf area. A linear correlation was observed between K_L and leaf area (Fig. 2C).
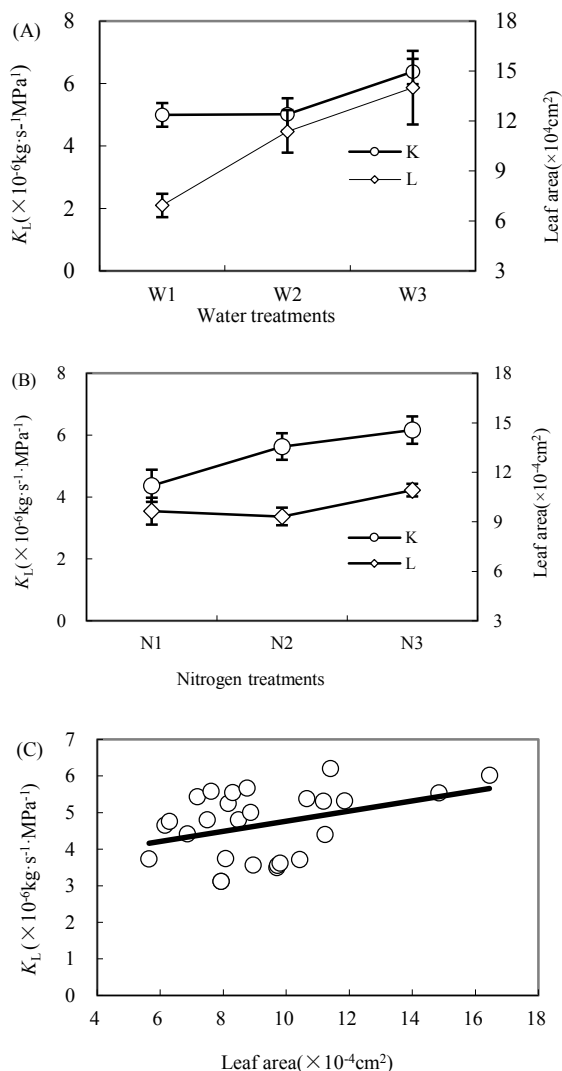
Diurnal variation of K_L and transpiration rate
Diurnal changes in K_L are shown in Fig. 3A. K_L showed a decreasing trend (the trend line indicates that the maximum was approximately 2.38×10^{-6} kg·s^{-1}·MPa^{-1}). K_L was higher, but not
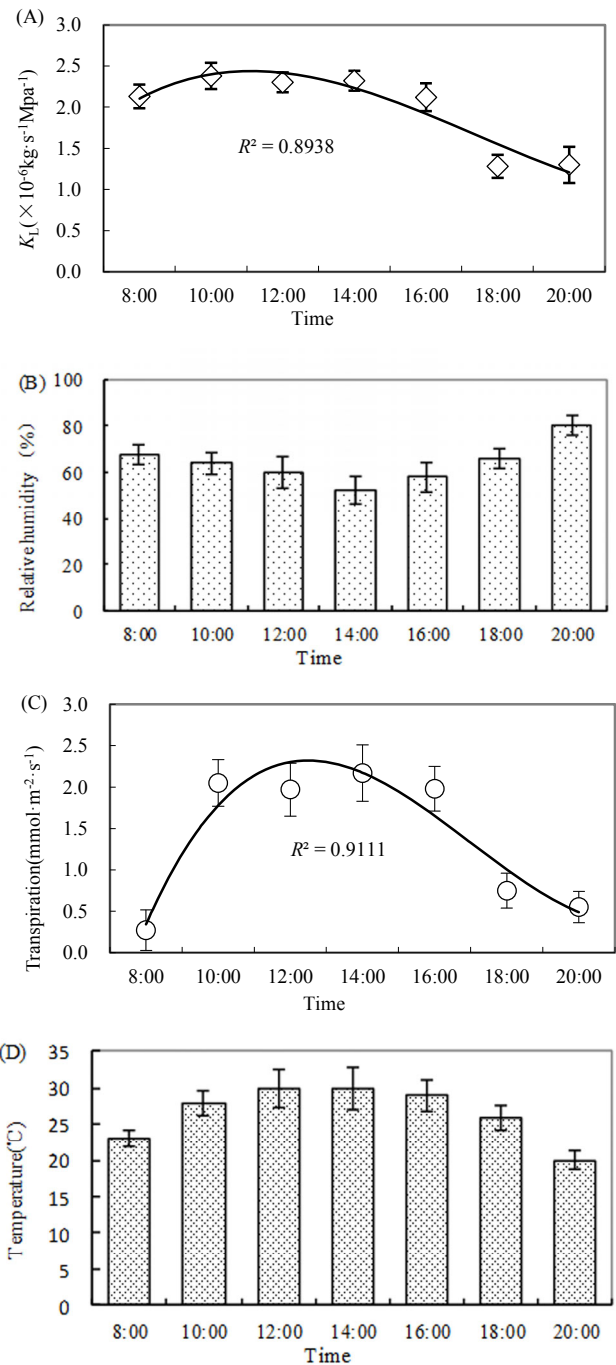
significantly, in the morning and began to decline sharply after 16:00. After 18:00, K_L declined until reaching its minimum at about 1.28×10^{-6} kg·s^{-1}·MPa^{-1} or 46% of the peak value

Diurnal changes in temperature and atmospheric relative humidity during the experimental period are shown in Fig. 3B and 3C. The daily maximum temperature was observed at noon and was held until 14:00. Relative humidity reached its daily minimum (about 52%) at about 14:00 and lagged behind the maximum temperature.

Diurnal variations in K_L and transpiration rate of peach seedlings are shown in Fig. 3. The transpiration rate was relatively slow at morning and evening. Maximum transpiration rate (approximately 2.5 mmol·m^{-2}·s^{-1}) was reached at noon. The change in transpiration rate plotted as a single-peak curve that began to decline sharply after 14:00 (Fig. 3C).

Fig. 2: Effect of soil water and nitrogen contents on the leaf hydraulic conductance (K_L; A) and the leaf area (B). Correlation between K_L and leaf area (C). W_1, W_2, and W_3 indicate that the average soil moisture conditions are 45% to 55%, 60% to 70%, and 75% to 80% of the field water capacity, respectively.

Fig. 3: Comparison of diurnal changes in the leaf hydraulic conductance (K_L) and the transpiration rate of peach seedlings. Data points are means ± standard errors ($n = 3$).

Root and shoot hydraulic characteristics

Root and shoot hydraulic conductivity

Table 1 shows the significant effects of N content and soil moisture on root diameter, shoot hydraulic conductivity (K_S), and root hydraulic conductivity (K_r). The excised root diameter increased with the lower soil moisture and was larger at W_1. No significant effects of N content were observed on excised root diameter at

W_1 and W_2, but significant effects were observed at W_3. At N_1, N_2, and N_3 treatments, the mean excised root diameter increased by 5.8%−12.5%, 6.1%−16% and 12.8%−20%, respectively, under W_3, W_2, and W_1 conditions, indicating that the excised root diameter increased at lower soil moisture content.

Table 1: Effect of N content on the excised root diameter, shoot hydraulic conductivity (K_s), and root hydraulic conductivity (K_r) of peach seedlings under different soil moisture conditions.

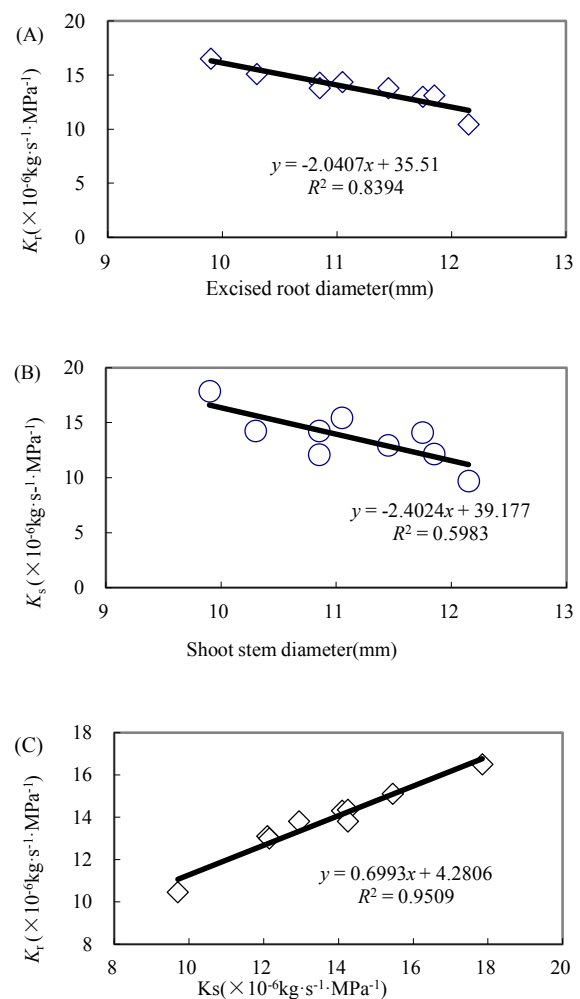| Water level	Nitrogen	Excised root diameter (mm)	Shoot hydraulic conductivity ($\times 10^{-6} kg \cdot s^{-1} \cdot MPa^{-1}$)	Root hydraulic conductivity ($\times 10^{-6} kg \cdot s^{-1} \cdot MPa^{-1}$)
W_1	N_1	1.17 ± 0.05a	9.70 ± 0.99e	10.45 ± 0.92f
	N_2	1.14 ± 0.02ab	12.15 ± 0.21d	13.00 ± 0.42e
	N_3	1.13 ± 0.02ab	14.10 ± 0.28c	14.30 ± 0.57c
W_2	N_1	1.10 ± 0.02abc	12.95 ± 0.21d	13.80 ± 0.28cd
	N_2	1.04 ± 0.05cd	14.25 ± 0.21c	14.35 ± 0.35bc
	N_3	1.06 ± 0.04bcd	15.45 ± 0.21b	15.10 ± 0.28b
W_3	N_1	1.04 ± 0.02cd	12.10 ± 0.28d	13.10 ± 0.57e
	N_2	0.98 ± 0.01de	14.25 ± 0.35c	13.80 ± 0.56cd
	N_3	0.94 ± 0.03e	17.85 ± 0.22a	16.50 ± 0.28a
Significance test (p value)				
Water level		<0.001	<0.001	<0.001
Nitrogen treatment		0.034	<0.001	<0.001
W×N		0.64	0.003	0.0014

Notes: Different letters in the same column indicate significant difference ($p < 0.05$). ANOVA P values are shown ($p < 0.05$, significance, $p < 0.01$, markedly significance, $p > 0.05$, no significance). Values are means ± SE (n = 3). N_1 is no fertilizer, N_2 is 0.15 $g \cdot kg^{-1}$, and N_3 is 0.3 $g \cdot kg^{-1}$.

Under identical soil moisture conditions, K_s and K_r increased with greater N content: K_s and K_r were both higher at N_3. K_s and K_r were lower at N_1 by 32% and 27%, respectively, but N_3 had no significant effect on K_s and K_r at W_1 (compared with controls). By contrast, K_s and K_r increased at N_1 (by 9.1% and 3.8%, respectively) and N_3 (by 8.4% and 5.2%, respectively) at W_2. At W_3, K_s and K_r also increased at N_1 (by 15% and 8.7%, respectively) and N_3 (25% and 15%, respectively). At N_2, W_1 seedlings showed K_s and K_r reduced by 14.7% and 9.4%, respectively, compared with controls. In contrast, W_3 showed no significant effect on K_s and K_r. Thus, increase in soil moisture and N content enhanced K_s and K_r. Moreover, this increase was enhanced to a larger extent under low soil moisture conditions, but the increase rate was gradually reduced with the increase in soil moisture.

Correlation between Kr and root diameter, Ks and shoot stem diameter, and Kr and Ks

Fig. 4 shows correlations between K_r and excised root diameter (Fig. 4A), K_s and shoot stem diameter (Fig. 4B), as well as between K_r and K_s (Fig. 4C) under different soil moisture conditions and N applications. K_r and K_s declined with increases in excised root diameter/shoot stem diameter under different soil water and N treatments. Linear negative correlations were observed between K_r and the excised root diameter as well as K_s

and the shoot stem diameter at different N applications and soil moisture conditions. K_r increased with the increase in K_s. Fig. 4C shows the positive correlation between K_r and K_s.

Fig. 4: Relationship between root hydraulic conductivity (K_r) and the excised root diameter (A), shoot hydraulic conductivity (K_s) and the shoot stem diameter (B), as well as K_r and K_s (C).

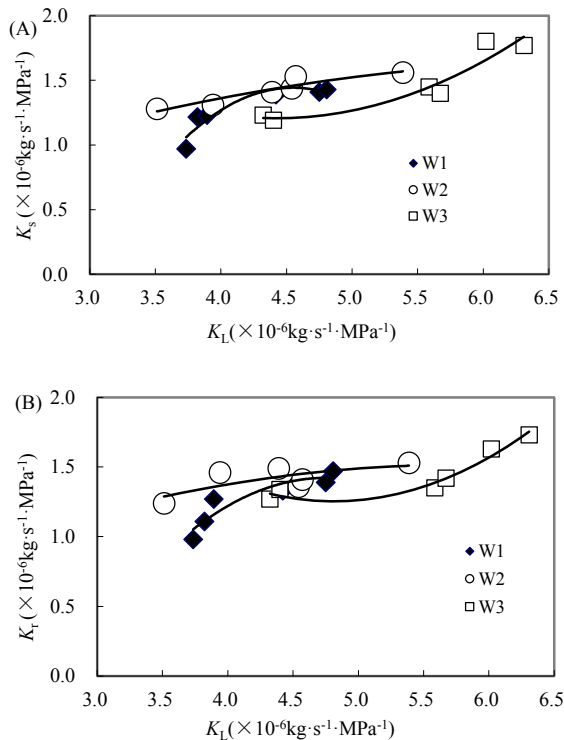*Relationship between K_L, K_r, and K_s under different soil moisture conditions*

Fig. 5 shows the correlations between K_s and K_L (Fig. 5A), and between K_r and K_L (Fig. 5B) under different soil moisture conditions. K_s increased as K_L increased. However, variations in the correlation curve were observed under different soil moisture conditions. The correlation curves between K_r and K_L under different soil moisture conditions were similar to the former case.

Growth and water consumption

Cumulative water consumption

Fig. 6 shows the cumulative water consumption curve of peach seedlings under different soil moisture conditions and N treatments from April to September. At W_3, N treatment showed no significant effect on cumulative total water consumption (9.59 L). Total water consumption increased and cumulative water con-

sumption increased significantly with increased soil moisture under different N treatments. Total water consumption also increased with increases in N fertilizer. At W_2 and W_3, the cumulative total water consumption for N_3 increased by 4.2% (14.85 L) and 6.25% (19.21 L), respectively, compared with N_1.

Fig. 5: Relationship between leaf hydraulic conductivity (K_L), root hydraulic conductivity (K_r), and shoot hydraulic conductivity (K_s) under different soil moisture conditions. W_1, W_2, and W_3 indicate that the average soil moisture conditions are 45% to 55%, 60% to 70%, and 75% to 80% of the field water capacity, respectively.
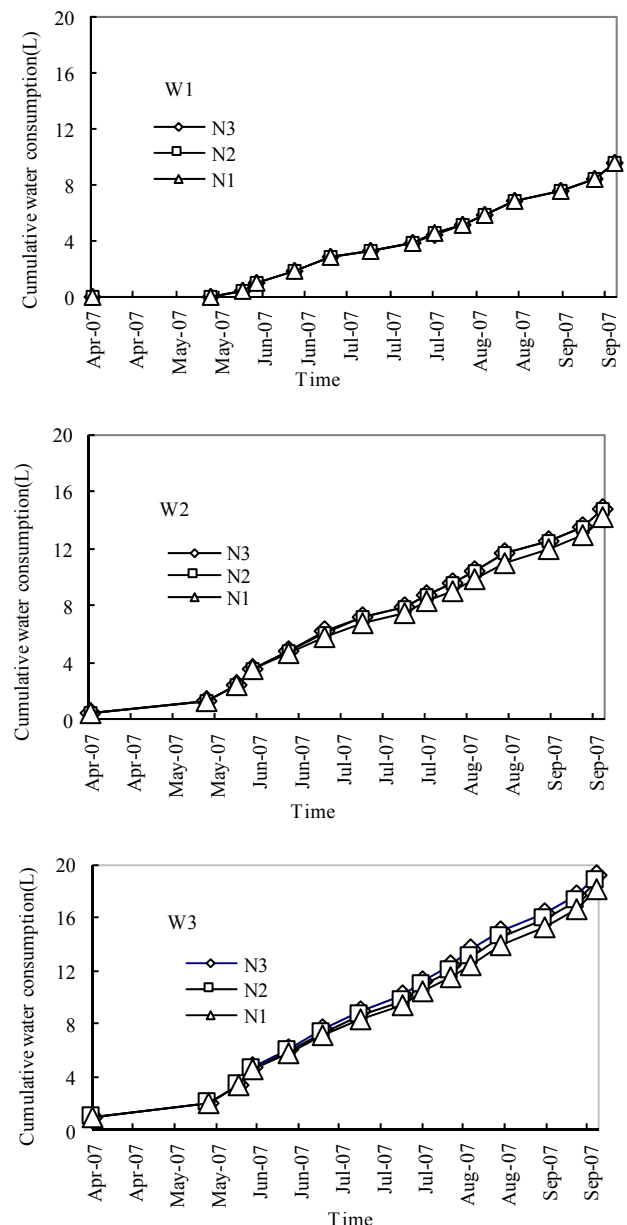
Root length and plant height

Soil moisture and N content had significant effects on root length, but no interaction effect was detected. Under identical soil moisture conditions, plant height and root length increased significantly with at increased amounts of N (Table 2). Soil moisture levels W_1 and W_2 yielded similar root lengths for any given N treatment. N_1, N_2, and N_3 treatments, however, yielded increases in root lengths of 36, 41, and 44%, respectively, at W_3 compared with CK.

An important effect of N content on plant height was recorded at different water treatments. In contrast, no significant effect on plant height was found in the other treatments except for W_1N_1 and W_3N_3 treatments, which yielded significant increases in plant height of 9.1% and 5.3%, respectively.

Dry mass accumulation and water-use efficiency

Shoot dry biomass at N_1 declined by 3.3% for W_1 and 2.3% for W_2 (Table 2). In contrast, shoot dry biomass increased under some combinations of treatments compared with controls (Table

2): 8.6% increase in W_3, 2.2% and 12.3% increase in W_1 and W_3 in N_2, respectively, and 11%, 10.8%, and 14% increase in W_1, W_2, and W_3 in N_3, respectively. Root dry biomass increased with larger N fertilizer application rates, but no significant difference was observed between N treatments under the same soil moisture condition. Root-to-shoot biomass ratios declined with increasing soil moisture, in which the root-to-shoot ratio initially increased slightly. Increased applications of nitrogen fertilizer yielded higher root-to-shoot ratios. In W_1, the root-to-shoot ratio for N_3 increased by 14% compared to N_1. The root-to-shoot ratio increased by 12 and 4.39% in W_2 and W_3, respectively.

Fig. 6: Effects of nitrogen content on cumulative water consumption of peach seedlings under different soil moisture conditions. N_1 is no fertilizer, N_2 is 0.15 g· kg^{-1}, and N_3 is 0.3 g· kg^{-1}. W_1, W_2, and W_3 indicate that the average soil moisture conditions are 45% to 55%, 60% to 70%, and 75% to 80% of the field water capacity, respectively.

Dry mass accumulation and water-use efficiency

Shoot dry biomass at N_1 declined by 3.3% for W_1 and 2.3% for W_2 (Table 2). In contrast, shoot dry biomass increased under some combinations of treatments compared with controls (Table 2): 8.6% increase in W_3, 2.2% and 12.3% increase in W_1 and W_3 in N_2, respectively, and 11%, 10.8%, and 14% increase in W_1, W_2, and W_3 in N_3, respectively. Root dry biomass increased with larger N fertilizer application rates, but no significant difference was observed between N treatments under the same soil moisture condition. Root-to-shoot biomass ratios declined with increasing soil moisture, in which the root-to-shoot ratio initially increased slightly. Increased applications of nitrogen fertilizer yielded higher root-to-shoot ratios. In W_1, the root-to-shoot ratio for N_3 increased by 14% compared to N_1. The root-to-shoot ratio increased by 12 and 4.39% in W_2 and W_3, respectively.

Significant effects of soil moisture and N content on water-use efficiency (WUE) were also observed. WUE declined with increases in soil moisture. The effects of N fertilizer on WUE were mainly related to soil moisture. The interaction between soil moisture and N also showed a significant influence on WUE. In particular, WUE at N_1, N_2, and N_3 in W_1 increased by 50, 57 and 69%, respectively, compared with controls. WUE increased by 9.9% at N_3, but showed no increase at N_1 treatment in W_2. The root dry biomass at N_1, N_2, and N_3 treatments declined by 11, 12, and 13%, respectively, in W_3.

Table 2: Peach seedling biomass and water-use efficiency (WUE) at the end of the experiment.

Water level	Nitrogen	Shoot dry biomass (g)	Root dry biomass (g)	Root length (cm)	Plant height (cm)	WUE (g·L^{-1})
W_1	N_1	40.20 ± 0.93d	26.49 ± 0.62c	30.50 ± 0.71e	66.60 ± 2.26d	6.96 ± 0.12e
	N_2	42.49 ± 0.84c	26.53 ± 0.37c	32.25 ± 0.35d	71.05 ± 1.48c	7.20 ± 0.14d
	N_3	46.16 ± 1.25ab	26.60 ± 0.36c	33.75 ± 0.35c	72.70 ± 0.99bc	7.59 ± 0.19c
W_2	N_1	40.64 ± 1.95d	26.96 ± 0.3ab	30.01 ± 0.11e	72.25 ± 1.77bc	4.74 ± 0.11e
	N_2	41.59 ± 1.73cd	26.73 ± 0.64bc	32.20 ± 0.28d	73.30 ± 1.84bc	4.60 ± 0.19d
	N_3	46.08 ± 1.24ab	26.98 ± 0.23ab	34.30 ± 0.99c	75.10 ± 1.56ab	4.92 ± 0.02c
W_3	N_1	45.16 ± 1.86b	26.97 ± 0.17ab	32.20 ± 0.37d	73.60 ± 0.57bc	3.99 ± 0.11b
	N_2	46.70 ± 1.67a	26.98 ± 0.24ab	45.25 ± 0.33a	74.05 ± 1.48b	3.94 ± 0.10a
	N_3	47.47 ± 0.93a	27.18 ± 0.35a	46.25 ± 0.35a	77.15 ± 1.20a	3.89 ± 0.09a
Significance test (*p* value)						
Water level		< 0.001	0.047	< 0.001	< 0.001	< 0.001
Nitrogen treatment		< 0.001	0.657	< 0.001	0.001	0.001
W×N		0.107	0.595	0.263	0.187	0.001

Notes: W_1, W_2, and W_3 indicate that the average soil moisture conditions are 45% to 55%, 60% to 70%, and 75% to 80% of the field water capacity, respectively. Values are means ± SE ($n = 3$). Different letters in the same column of the mean indicate significant differences ($p < 0.05$, significance, $p < 0.01$, markedly significance, $p > 0.05$, no significance) between the three nitrogen treatments with respect to the same water levels. We selected the homogeneous peach seedlings and obtained the average dry weight (average value = 20.23 g) before the seedlings were transplanted. The average dry weight was used as the benchmark value to calculate the growth of the seedlings. N_1 is no fertilizer, N_2 is 0.15 g·kg^{-1}, and N_3 is 0.3 g·kg^{-1}.

Discussion

Leaf hydraulic conductivity (K_L)

The main resistances of the plant water transport system are located in the leaves (Sack et al. 2006; Charra-Vaskou et al. 2011). Leaf resistance contributes approximately 30% and 80% to total plant resistance (Tyree et al. 1981; Yang and Tyree 1994; Sack et al. 2003; Sack and Holbrook 2006). Nardini and Salleo (2000) reported that 92% of the resistance in *Laurus nobilis* is found in the leaves. K_L, a major determinant of plant water transport capacity, is defined as the water flow rate per unit leaf area divided by the pressure decrease that drives the flow (Tyree and Nardini 2005). Leaves comprise a very significant proportion of the whole plant hydraulic pathway (Sack et al. 2003) and are often more vulnerable to water stress than other plant organs (Brodribb et al. 2003; Sack and Holbrook 2006;

Hao et al. 2008; Blackman et al. 2012). Thus, leaves might play a disproportionally large role in plant adaptation to drought (Hao et al. 2008).

Our findings indicated that leaf area and K_L were increased significantly in seedlings in response to increases in soil moisture and N content (Fig. 1). K_L was relatively high in the morning and began to decline significantly after 16:00 (Fig. 2). During morning, K_L declined after an initial increase but without a significant difference. The daily maximum temperature was observed at noon. The seedlings were not prone to cavitations in the morning because of low temperature and higher relative humidity. On one hand, K_L is an index that indicates the capacity of water transport and consumption, and is affected by soil moisture and fertilizer. Water that flows through the leaves has significant implications for plant hydraulics and plant growth as well as leaf structure, function, and ecology (Hernández et al. 2009). Therefore, water loss from the leaves should be minimized to avoid interruption of water flow in the xylem under severe drought (Burghardt and Riederer 2003). Moreover, reductions in the stomatal aperture to

avoid excessive water losses can increase WUE at the leaf level and has an important function in plant response to drought (Cochard et al. 2004; Agele et al. 2005). On the other hand, K_L is closely related to irradiance and temperature. Irradiance has a significant effect on stomatal aperture, and K_L can be enhanced by light (Tyree et al. 2005). Sack et al. (2002) demonstrated that K_L values obtained via HPFM are sensitive to irradiance, and low K_L values determined under low irradiance may be caused by stomatal closure. A previous study revealed that K_L in bur oak (*Quercus macrocarpa* Michx.) increased significantly when exposed to high irradiance. In addition, certain plant species grown under low irradiance can have lower K_L (Engelbrecht et al. 2000), and shaded leaves have lower K_L than sunlit leaves under given plant canopies (Sack et al. 2003, 2005; Lo Gullo et al. 2004). In this study, the transpiration rate of approximately 0.272 mmol·m^{-2}·s^{-1} was very low. However, transpiration rate (Tr_{max} = 2.17 mmol·m^{-2}·s^{-1}) and water loss increased significantly with increasing temperature. This phenomenon may produce xylem cavitations and embolism, thereby influencing water transport. As in stem xylem, water stress can cause a further increase in leaf hydraulic resistance when the leaf xylem is embolized (Charra-Vaskou et al. 2011). Xylem embolism directly reduces xylem hydraulic conductivity, thereby influencing normal plant physiological activities and survival. Our results are in agreement with previous findings with regard to the effect of temperature on hydraulic conductivity (K) and water relationship of *Q. robur* (Cochard et al. 2000).

In addition, K_L is highly variable and dynamic during plant life with patterns specific to each species (Nardini et al. 2010). K_L can vary up to 65-fold across plant species (Sack et al. 2005) and it can also vary depending on the anatomy and developmental stage of the leaf (Prado et al. 2013). K_L increases in developing leaves as the vasculature matures. In the weeks or months following its maximum, K_L begins to decline by up to 80%–90% at abscission (Brodribb et al. 2005). Some authors have hypothesized that seasonal decline of K_L is a trigger for leaf senescence (Sack and Holbrook 2006). Factors that affect hydraulic conductivity numerous and complex. Further study is needed to understand the mechanisms of plant water transport.

Root and shoot hydraulic characteristics

K of the unit pressure gradient, one of the most commonly measured parameters, is equal to the ratio of the water flow (F, kg·s^{-1}) through an isolated stem section to the pressure gradient that causes water to flow through the stem (dp/dx, MPa·m^{-1}), thus, $K = F/ (dp/ dx)$ and F is proportional to K. Under similar conditions, F increases with increasing stem diameter. Thus, water transport capacity is greater through thicker isolated stems with higher K. However, our results are different. Kr and Ks declined with increasing excised root/shoot diameter under various soil water and N treatments (Figs. 3A and 3B). Linear negative correlations were found between Kr and excised root diameter as well as Ks and shoot stem diameter. The following explanations might account for this result: (1) Changes in soil moisture result in different biomass allocations, root diameter de-

clines with increasing soil moisture, but enhances vertical root growth in the soil profile (Mambani et al. 1983; Cairnsa et al. 2011), thereby allowing access to a greater volume of soil water during periods of water deficit and enhancing root water transport. Fertilizer enhancement patterns of K closely match those observed for plant growth (Lovelock et al. 2004); (2) We recorded variation in Ks and Kr under different soil moisture conditions and N contents (Table 1). Ks and Kr increased with increased soil moisture under the same N treatment. Maximum Ks and Kr were obtained at W_3. Previous studies showed that Kr can decline to varying degrees (*c.* 50% to 70%) under soil drought condition primarily because the increased suberization of the periderm reduces radial conductivity (North and Nobel 1994). Thus, the declines in Kr during drought reduce plant water loss in dry soil. Drought stress can significantly reduce xylem K through cavitation (Cochard et al. 1996; Sperry et al. 1988) and might influence Kr. Plants tend to control the root water uptake and/or tissue water status under water deficit conditions by adjusting Kr (Maurel et al. 2008; Parent et al. 2009). However, the effects of drought on Kr depend on stress level (Siemens and Zwiazeck, 2004) and plant genotype. Several factors regulate Kr mainly by affecting the activity and/or abundance of water channel proteins (aquaporins) (Javot and Maurel 2002; Luu and Maurel 2005). Plants can actively accumulate low-molecular weight substances such as water-soluble molecules when subjected to water stress, and these substances can regulate the osmotic potential of plants according to the law of mass action to enhance water-holding capacity and reduce osmotic stress (Song and Wang 2002), thereby decreasing K.

Ks is greatly influenced by fertilizers. N fertilizers improve Kr, and thus increase the transpiration rate, stomatal conductance, and photosynthetic rate (Clarkson et al. 2000; Trubat et al. 2006). Lovelock (2004) found that N has the most significant effect on Ks, which can increase 2- to 5-fold with N enrichment. In this study, the effect of soil moisture and N interaction on Ks and Kr also reached a significant level. Soil moisture and N fertilizer are coupling parameters that can promote each other and function cooperatively.

In the whole water transport process, the root system still represents a significant barrier although water flow resistance through plants is due to the stomatal aperture (Steudle et al. 1998) and thus can contribute to approximately 50% of the overall hydraulic resistance of the plant (Martre et al. 2001). Previous research showed that the contribution of the root system to total plant resistance ranges from 20% to 90% (Tsuda and Tyree 1997). Consequently, the root is considered a critical link in the soil-plant-atmosphere continuum (Javot and Maurel 2002). In this study, the contribution of the root system contribution to total hydraulic conductivity was approximately 41% (Fig. 3C).

Growth and water use

Plants reduce shoot growth during periods of water deficit (Boris Parent et al. 2009), and this leads to increased mass allocation to the roots (Tyree et al. 1998). In this study, the application of N fertilizer promoted rapid growth of shoots and reduced their N

content, thereby resulting in higher dry matter allocation to the roots. The root-to-shoot ratio declined with increased soil moisture. This result is consistent with earlier findings, in which biomass allocation is promoted below the ground under limited soil water conditions (Hacke et al. 2000; Martin, 2010; Paponov et al. 2000; Addington et al. 2006; Klein et al. 2011). In this study, the shoot-to-root ratio increased with increasing N applications. In W_1, the shoot-to-root ratio at N_3 increased by 14% compared to N_1. The shoot-to-root ratio also increased in W_2 and W_3 by 12% and 4.39%, respectively. Lovelock et al. (2004) showed that shoot growth is doubled when plants are treated with N fertilizer under nutrient-deficient conditions. These findings are qualitatively supported by our results. Soil penetration resistance also influences root growth by exhibiting a more fundamental constraint to root growth than soil water availability (Cairns et al. 2004).

For six months of the growth period, we found no significant influence of N fertilizer application on water consumption under low soil moisture conditions. Total water consumption increased with increased N application and increased soil moisture. WUE declined with increased soil moisture and the effects of N fertilizer on WUE were mainly related to soil moisture. In particular, a positive effect of N fertilizer on WUE was observed under low soil moisture conditions, but no significant influence was observed under high soil moisture conditions. Under normal water supply, WUE was higher at high N treatment (N_3), increasing by 9.87% over controls.

Conclusions

We confirmed that plant growth, biomass allocation patterns, K (shoot, root, and leaf), and WUE varied in peach seedlings. Soil moisture and N fertilizer conditions influenced the hydraulic characteristics (K_s, K_r, and K_L) of peach seedlings. K (root, shoot, and leaf) was enhanced under moderate N conditions, which elicited a significant effect on the growth of the seedlings (such as leaf area, stem diameter, and shoot-to-root ratio). A positive effect of N fertilizer on WUE was observed under low soil moisture conditions, but no significant influence was observed under high soil moisture conditions.

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